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Long-term changes in a zooplankton community revealed by the sediment archive

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Abstract

To reconstruct changes in zooplankton communities in response to past anthropogenic perturbations, one possibility is to use the sedimentary records. We analyzed the sediments at a coastal site in the Northern Baltic Sea to relate changes in the zooplankton community to anthropogenic eutrophication and the invasion of a predatory cladoceran, *Cercopagis pengoi*. We sampled 30-cm laminated sediment cores and dated the sediment layers back to the 1950s. From each 1-cm layer, we measured eutrophication indicators (δ^{13}C, δ^{15}N, TC, TN, TP) and identified and counted zooplankton resting eggs (cladoceran, calanoid copepod, rotifer). In addition, we estimated the abundance of the cladoceran *Bosmina* (*Eubosmina*) *maritima* by counting subfossils (carapaces, headshields, and ephippia) and estimated the experienced stress as the relationship between sexual and asexual reproduction. Using redundancy and variance partitioning analyses, we found ~ 16% of the variation in the zooplankton community to be explained by eutrophication, and 24% of the variation in *B.* (*E.*) *maritima* abundance and reproduction mode to be explained by eutrophication and the introduction of the alien predator. Our results show a long-term shift from calanoid copepods and predatory cladocerans toward small-sized zooplankton species, like rotifers. Furthermore, the results indicate that the invasion of *C. pengoi* induced a short-term increase in sexual reproduction in *B.* (*E.*) *maritima*. The results indicate that anthropogenic eutrophication since the 1950s has altered the zooplankton community toward smaller species, while the invasion of the predatory cladoceran had only a transitory influence on the community during its expansion phase.

Humans are altering environmental conditions at an unprecedented rate and scale. This is in turn altering species communities, but the mechanisms behind the effects, and how the changes progress over time, are poorly known (Walther 2010; Bellard et al. 2012; Moritz and Agudo 2013; Dirzo et al. 2014; Scheffers et al. 2016). This is hampering our understanding of the long-term consequences of anthropogenic disturbances for ecosystem structure and function. A promising avenue for investigating past responses of communities to environmental changes is to use paleobiological data. In particular, the sediment archives can provide valuable information by shedding light on community responses to perturbations, identifying sensitive species–species interactions, and improving our understanding of the mechanisms and processes behind the changes (Jackson and Blois 2015; Kidwell 2015; Maguire et al. 2015; Barnosky et al. 2017). The information can, in turn, be used to test and refine models of how biota will respond to future environmental changes (Dietl et al. 2015).

Coastal areas are one of the most heavily impacted ecosystems in the world (Kennish 2002). Human-induced eutrophication has promoted primary production with dramatic consequences for nutrient cycling, oxygen conditions, habitat structure, and species diversity at all trophic levels. Similarly, climate change, overfishing, and the introduction of nonindigenous species have caused alterations to the distribution and abundance of species (Cloern 2001; Harley et al. 2006; Levin et al. 2009). A fascinating possibility is to use the archives hidden in the sediments to study past changes in aquatic communities. Seabeds with undisturbed, laminated sediment—because of hypoxia that excludes burrowing benthic fauna—can be dated, and the abundance and morphology of species that leave remains in the sediment, such as exoskeleton or dormant life stages, can be determined (Brendonck and De

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Meester 2003). In addition, various proxy variables of environmental factors can be used to reconstruct past changes in conditions, like nutrient levels.

Many zooplankton taxa produce resting eggs that can stay viable for decades, even centuries, in the sediments (De Stasio 1989; Hairston et al. 1995). These are produced to ensure survival over harsh periods or seasons, and they remain dormant if they do not receive the right stimuli for hatching or their development is hampered by hypoxia (Warner and Chesson 1985; Hairston 1996). Such "egg banks" may not be perfect reflections of the community of species at the time when they were deposited, or even of what was deposited, as species and populations vary in the production of resting eggs or in the demands for hatching, and as some resting eggs may be lost via mixing, degradation, predation, and senescence (De Stasio 1989). However, they give an indication of the composition of the community at the time when the sediment layer was formed. In addition, some zooplankton taxa leave subfossils that can be counted for abundance estimates and measured for morphological traits (Korosi et al. 2013).

The Baltic Sea is an area that has undergone major human-induced environmental changes during the last decades. Eutrophication has intensified since the 1950s, and much of the sea is currently severely affected (Elmgren 2001; Andersen et al. 2017). In addition, overfishing, climate change, and the invasion of nonindigenous species have altered the environment. The Baltic Sea is especially vulnerable to disturbances as it is a relatively young sea that has undergone both fresh and saline phases after the Holocene ice sheet receded 11–10 ka BP. In addition, winter ice cover and brackish water, which exclude many marine and freshwater species, contribute to the low biodiversity (Ojaveer et al. 2010).

A recent invader to the Baltic Sea that could influence the zooplankton community is the fishhook waterflea *Cercopagis pengoi*, as it predates on other zooplankton (Ojaveer and Kotta 2015). It is native to the Ponto-Caspian region and it was first found in the Baltic Sea in 1992, after which it rapidly spread and established itself in the sea (Ojaveer et al. 2000). It reproduces through parthenogenesis under favorable conditions, and through sexual resting eggs when conditions deteriorate in the fall. The abundance of the resting eggs in the sediment can be used to determine the invasion history of the species (Katajisto et al. 2013).

We used the zooplankton "egg bank" at a coastal site in the northern Baltic Sea to investigate whether changes in the zooplankton community correlate with environmental changes, particularly with eutrophication and the invasion of the predatory water flea *C. pengoi*. The studied area has had laminated sediment at least from 1950–1960s to the 2000s (Vallius 2006), which allowed us to date the sediment and use resting eggs to estimate changes in the zooplankton community of cladocerans, copepods and rotifers. For the most common cladoceran, the endemic *Bosmina* (*Eubosmina*) *maritima*, (also known as *Bosmina coregoni maritima*, *B. longispina maritima*, and *E. maritima*; e.g., Purasjoki 1958; Kankaala and Wulff 1981; Kotov et al. 2009; Błędzki and Rybak 2016), we investigated correlations between environmental changes and abundance, as well as its relative use of sexual and asexual reproduction, as sexual reproduction can be an indication of stress in cyclically parthenogenetic cladocerans (Decaestecker et al. 2009). To estimate abundance, we counted carapaces and headshields and to estimate the abundance of sexually reproducing individuals, we counted ephippia (the shells that enclose the resting eggs). *B.* (*E.*) *maritima* is most abundant in the shallow coastal areas (Kankaala and Wulff 1981), but occurs also in the open sea areas (Suikkanen et al. 2013). It is a cyclic parthenogen with several generations of parthenogenic females followed by sexual females and males, which produce fertilized resting eggs. These overwinter in the sediment, enclosed in the ephippia, from which they hatch after a latent period, usually in spring or early summer (Kankaala 1983).

Materials

Study site

Sampling was done in Sandöfjärden in the archipelago of Tammisaari in the western part of the Gulf of Finland (59°53′683″N 23°36′394″E) (Fig. 1). The sampling site is ~ 27-m deep, and the water layers close to the sediment are periodically hypoxic or anoxic (Finnish Environment Institute, Hertta database). This is because oxygen is consumed by decomposition of sedimenting organic material such as decaying algal blooms and topography that restricts the replacement of deep-water layers until fall convective mixing. Surface water salinity is on average 5.7 and near seabed salinity 6.0. Water temperature near the seabed fluctuates between 4°C and 10°C seasonally.

Sediment sampling

Sampling was conducted in early May in 2013 after ice melt using a GEMAX twin gravity corer with an inner liner diameter of 9 cm. Four 30-cm long sediment cores were sliced into 1-cm samples and stored in plastic boxes at 3°C in the dark, with a plastic foil on top of each sample to avoid oxygenation of the surface.

Sediment dating and sediment-derived environmental data

To date the sediment, the samples from one core were weighed for wet weight to the nearest 0.0001 g, dried for 4 d at − 60°C (Thermo electron corporation, SuperModulyo), and weighed again to the nearest 0.0001 g. Homogenized freeze-dried samples were measured for ^{137}Cs by gamma spectrometry (Geological Survey of Finland). Age was estimated by locating the ^{137}Cs peak created by the Chernobyl nuclear plant accident in April 1986, and by the lower peaks created

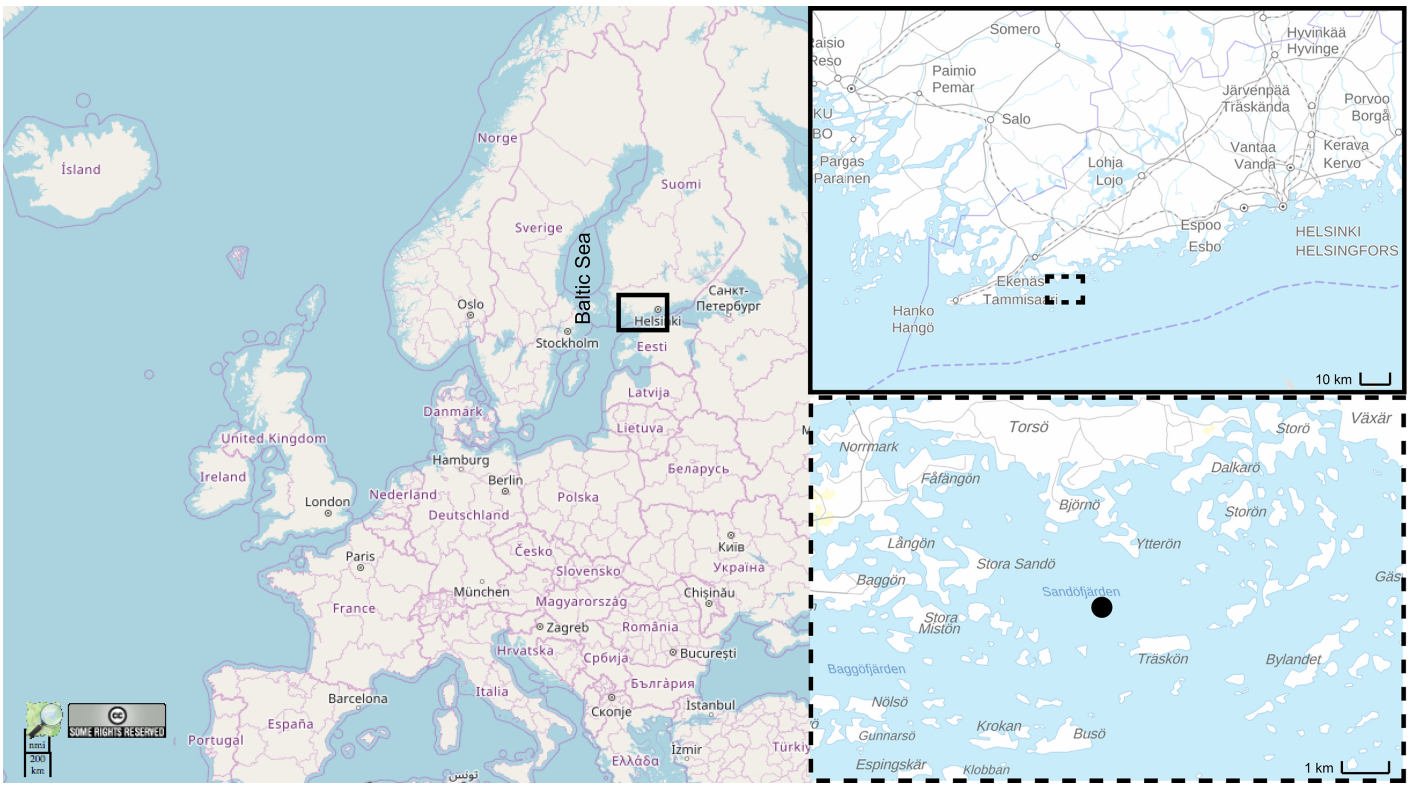

Fig. 1. Map showing the sediment sampling site Sandöfjärden at the South Coast of Finland, Baltic Sea, Europe. © OpenStreetMap contributors and National Land Survey of Finland.

by the testing of atmospheric weapons in the Pacific Ocean in the 1960s.

To determine nutrient levels and primary production during the recorded time period, total carbon (TC), total nitrogen (TN), and the stable isotopes $\delta^{13}C$ and $\delta^{15}N$ were measured from the freeze-dried sediment samples by mass spectrometry (Europa Scientific TracerMass, ANCA-MS 20-20). TC is almost completely made up of organic carbon in the Gulf of Finland (Carman and Cederwall 2001), and acidification of the samples with HCl was therefore not performed. Total phosphorus (TP) and organic phosphorus (OP) were measured by adding 0.017 M $MgSO_4$ to the freeze dried samples (Solórzano and Sharp 1980), drying at 95°C, burning at 450–500°C for 2 h, shaking overnight in 1 M HCl, and analyzing with spectrophotometer (Koroleff 1976).

Zooplankton resting eggs

From the second sediment core, parallel to the dated core, resting eggs, the "egg bank," were investigated. The sediment samples were sonicated in ultra sound bath for 7 min and sieved using 150 μm and 48 μm sieves and filtered sea water (Whatman GF/C, nominal pore size 1.2 μm). The remaining materials (fractions >50 μm and >150 μm) were centrifuged (3000 rpm (2000 g) for 3 min) in sugar solution, with 1000 g sucrose in 1000 mL MilliQ-water. The supernatant of both fractions was sieved once more with a 50-μm sieve and washed carefully with filtered sea water. A Leica MZ12 stereomicroscope was used for the identification and counting of water flea ($>$ 150 μm), and copepod and rotifer ($>$ 50 μm) resting eggs in each 1-cm sample.

Species identification was based on Viitasalo and Katajisto (1994). Calanoid copepod resting eggs could not be identified to species level in the oldest layers and were combined as *Calanoida* spp. Cladoceran resting eggs were identified to genus level for *Ceriodaphnia* spp., *Daphnia* spp., *Pleopsis* and *Podon* spp.; to species level for *C. pengoi*, *B.* (*E.*) *maritima*, and *Evadne nordmanni*. Some *Ceriodaphnia* spp., *Daphnia* spp., or *B. (E.) maritima* resting eggs had lost their ephippia, which made identification uncertain. These were grouped as *Cladocera* spp. Rotifer resting eggs were identified to genus level, *Keratella* spp. and *Synchaeta* spp.

Bosmina (*Eubosmina*) *maritima* subfossils

The abundance and sexual reproduction of *B.* (*E.*) *maritima* was determined from subsamples (4–10 g) of each 1-cm sample of the third sediment core. Subfossil samples were prepared according to Korhola and Rautio (2001), and identified and counted using a Hydro-Bios Standard Counting Chamber for Zooplankton (22 mL) and Leica M-series stereomicroscopes, with maximum magnification of 100–160×. For each 1-cm sample interval, at least 200 headshields and carapaces, and 50 ephippia were counted and related to

volume examined to calculate abundances. Adult female carapaces were separated from juveniles and males by their shape (K. Van Damme unpubl.), and the ratio of ephippia to adult female carapaces, which indicates the prevalence of sexual to asexual reproduction, was calculated.

Water quality monitoring data

In addition to the environmental data extracted from the first sediment core, water quality monitoring data from Sandöfjärden and three close by sampling stations; Längden (59°46′421″N 23°15′697″E), Skogbyfjärden (59°92′028″N 23°33′212″E), and Storfjärden (59°85′557″N 23°26′533″E) (Finnish Environment Institute, Hertta database) were collected to get as extensive a data set as possible for the investigated period. The extracted variables were chlorophyll *a* (Chl *a*, indicates primary production), water temperature, and salinity at the depth of 5 m ± 1 m. Monthly anomalies for Chl *a*, salinity, and temperature were calculated for the time period available, from June 1974 until April 2013 and were averaged for fall (September–November), spring (March–May), and summer (June–August). Three alternative dating models were formed, using second degree polynomial functions, depending on the locations of the ^{137}Cs peaks created by the Chernobyl nuclear accident and the nuclear weapons testing in the Pacific Ocean within the 1-cm sediment layers, i.e., did they happen during formation of top, middle, or bottom of the 1-cm layers. Average summer Chl *a* anomalies were calculated for each sediment layer using the different dating models and correlated with the corresponding TC measurements, which indicate primary production during the formation of the sediment layer. The dating model with the highest correlation between Chl *a* and TC was chosen for further analyses. The period from January 1980 to May 1987 contained too few data points for Chl *a* or salinity and the corresponding sediment layers (13, 17, 18, and 19 cm) were therefore excluded from the analyses.

Statistical analysis

The relative abundances of resting eggs of each taxon in each 1-cm sample were calculated. To determine correlations between sediment derived environmental variables and zooplankton community composition, the upper 5 cm were excluded from the analyses, as these layers are not comparable to deeper layers for environmental variables, because of a higher content of nondegraded material (Cornwell et al. 1996; Vaalgamaa and Korhola 2007). In the models using monitored water quality data, only the upper 1 cm was excluded from the models, since it was an outlier in the "egg bank" data.

All statistical analyses were performed using R version 3.0.2 (R Core Team 2016). Two alternative statistical models were constructed to analyze changes in the zooplankton egg bank as well as in the *Bosmina* population: (1) a "sediment model" using sediment-derived eutrophication indicators as explanatory variables, (2) a "monitoring model" using Chl *a*, salinity, and water temperature monitoring data as explanatory variables. To take the possible autocorrelation between the sediment layers into account, sample depth was used as an explanatory variable, and variance partitioning was made to separate between temporal autocorrelation and environmental effects (Birks 2012). Variance inflation factor (VIF) values were checked for possible collinearity between the sediment derived eutrophication indicators and sediment depth (Zuur et al. 2009), and the list of explanatory variables in the sediment models was shortened to sediment depth, δ^{13}C, δ^{15}N, C : N, C : P. In addition, the introduction of the predatory cladoceran *C. pengoi* (resting egg abundance) was used as an explanatory variable in the sediment model used to describe changes in *Bosmina* population.

To ascertain how the zooplankton community and the *Bosmina* population have changed through time relative to environmental variables, multivariate methods available in the vegan package (Oksanen et al. 2016) were used. To check if linear constrained ordination methods, such as redundancy analysis (RDA) and distance-based redundancy analysis (db-RDA) (Legendre and Anderson 1999) were appropriate, an initial detrended correspondence analysis (DCA) was applied. The gradient lengths of the first two axes were shorter than three standard deviation units, which indicate that the data is not too heterogeneous for linear models. Relative species abundances were square root transformed in order to reduce heterogeneity. Because the data contained several zero-values, a db-RDA was used to relate relative species abundances to environmental variables. Db-RDA detects linear relationships when distance measures are nonlinear. It calculates a distance matrix based on a non-Euclidean distance measure, the Jaccard distance measure in this study, which is transformed using principal coordinate analysis (PCoA) to a set of principal coordinates in Euclidean space. These were analyzed using standard RDA and permutation test with 999 permutations.

To investigate if the variation in the *Bosmina* population can be explained by eutrophication and the introduction of *C. pengoi*, we related abundance of the subfossils to the environmental data determined from the sediment layers (the sediment model), and to the monitoring data (the monitoring model), using RDA and square-root transformed *Bosmina* data. RDA allows regression of multiple response variables on multiple explanatory variables when the expected relationship is linear (Legendre and Legendre 1998). It generates a matrix of the fitted values of all response variables, which is subjected to a principal component analysis. The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations).

Results

Sediment properties and dating

The sediment cores were partially laminated with oxygenized brownish layers alternating with anoxic dark gray layers.

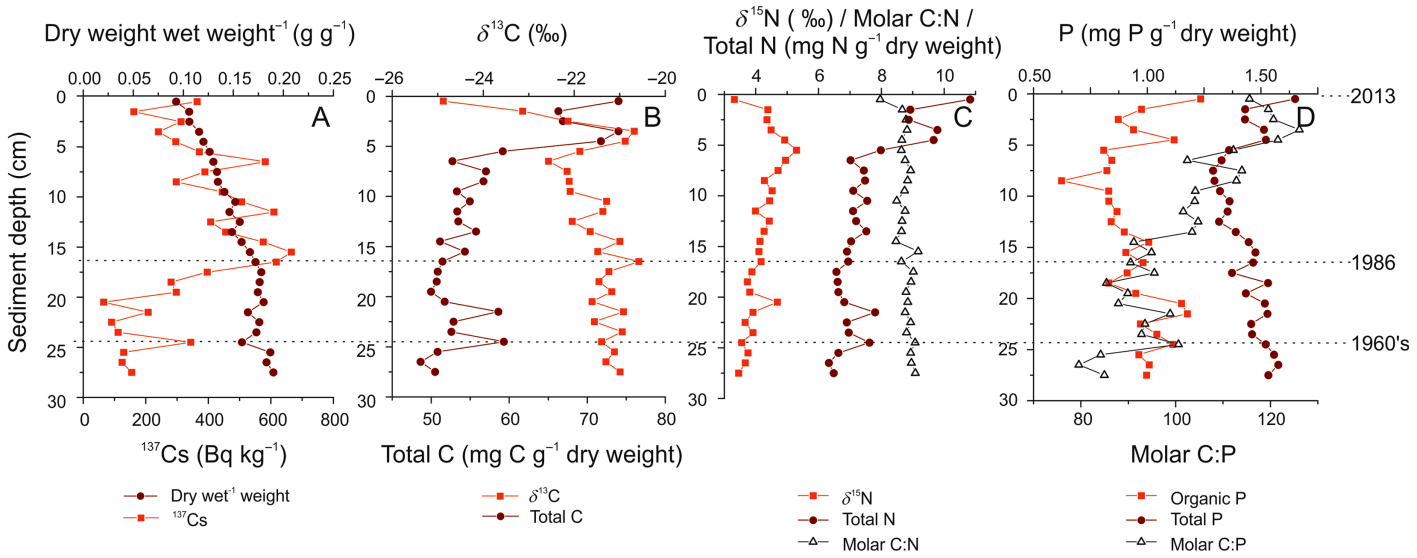

Fig. 2. Sediment properties and eutrophication indicators. Sediment profiles for (**A**) the ratio of sediment wet weight/dry weight, as well as ^{137}Cs loadings, (**B**) total organic nitrogen, C : N ration, and the stable isotope δ^{15}N, C) TOC and the stable isotope δ^{13}C, of Sandöfjärden Gulf of Finland, Baltic Sea.

The dry weight of the sediment samples decreases steadily toward surface layers (Fig. 2A); while wet weights do not, but vary between 1.01 g cm^{-3} and 1.11 g cm^{-3}, excluding the upper 1 cm.

The ^{137}Cs concentrations in the sediment layers indicate some degree of mixing, which could result from the sampling procedure, from burrowing animals, or from mobility of ^{137}Cs in sediments. Yet, there are two clear peaks: at sediment depth 16–17 cm, which indicates the Chernobyl nuclear plant accident, and at 24–25 cm depth, which probably indicates the testing of atmospheric nuclear weapons in the Pacific Ocean in the 1960s (Fig. 2A). This indicates that the layers date back to the 1950s. The more recent sediment layers cover shorter time periods than the deeper layers.

Eutrophication indicators

The sediment profiles below the upper most 5 cm reveal that the quantity of sedimenting carbon (TC) and nitrogen (TN) has increased gradually over the past decades. Concentration of TC in the dry sediment are slightly lower at depths 24–28 cm (52.4 mg g^{-1} ± 1.8 mg g^{-1}, mean ± SE) than at depths 6–10 cm (55.8 mg g^{-1} ± 1.2 mg g^{-1}), although two highly productive layers are found also at 22 cm and 25 cm depths (Fig. 2B). The δ^{13}C stable isotope ratio varies between − 22.6‰ and − 20.6‰ with no clear trend over time (Fig. 2B). Concentration of TN increases from 6.81 mg g^{-1} ± 0.23 mg g^{-1} at depths 24–28 cm to 7.41 mg g^{-1} ± 0.17 mg g^{-1} at depths 6–10 cm (Fig. 1C). The TC : TN ratio shows a slightly decreasing trend toward the surface with an average of 7.69 ± 0.04 at depths 24–28 cm and 7.53 ± 0.04 at depths 6–10 cm (Fig. 2C). δ^{15}N increases constantly until 6-cm depth, being 0.367‰ ± 0.008‰ at depths 24–28 cm and 0.475‰ ± 0.017‰ at depths 6–10 cm (Fig. 2C). TP and OP content show opposite patterns to that of TC and TN; both have decreasing trends toward the surface, apart from the surface sediment (Fig. 2D). Concentration of TP is 1.53 mg g^{-1} ± 0.02 mg g^{-1} at 24–28 cm and 1.32 mg g^{-1} ± 0.01 mg g^{-1} at depths 6–10 cm, and concentration of OP is 1.02 mg g^{-1} ± 0.03 mg g^{-1} at 24–28 cm and 0.79 mg g^{-1} ± 0.04 mg g^{-1} at 6–10 cm. The ratio TC : TP increases toward the surface from 88.4 ± 3.7 at depths 24–28 cm to 109.1 ± 2.4 at 6–10 cm (Fig. 2D).

Zooplankton egg bank and its relation to eutrophication

Calanoid copepod resting eggs are present throughout the sediment layers, with abundance being highest in the 1-cm surface sediment—over 10-fold compared to the other sediment layers and constituting almost 70% of the all the resting eggs found in that layer (Fig. 3A). When excluding the surface layer, sediment layers with the highest relative frequency of calanoid resting eggs are <20 cm. At the depth of 20–25 cm, the copepod resting eggs constitute the majority of the resting eggs. It thus seems that their contribution to the overall zooplankton resting eggs composition has decreased with time.

The most abundant cladoceran resting eggs are the predatory water fleas *Pleopsis* and *Podon* spp. and *E. nordmanni*. They are less abundant than the smaller copepod and rotifer resting eggs but their summed relative abundance is usually over 20%, apart from the uppermost 10 cm of the sediment core (Fig. 3A). Their contribution to the total zooplankton resting egg composition has thus decreased with time. The dominance between the two cladoceran taxa shifts in the lower sediment layers, with *Evadne* dominating under 17 cm,

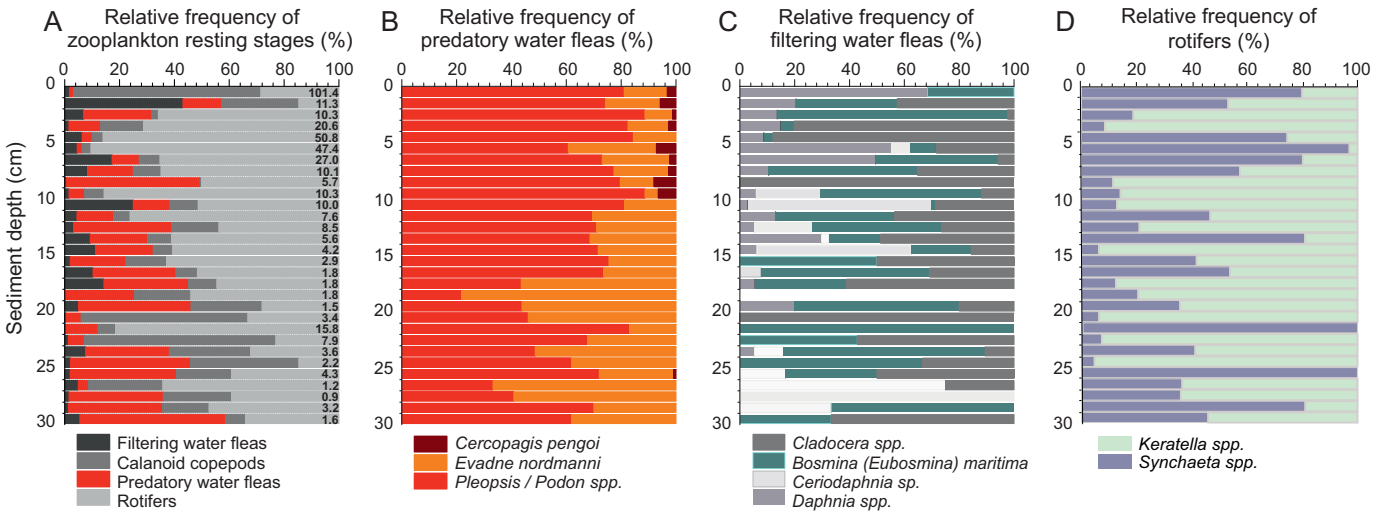

Fig. 3. Zooplankton egg bank. Relative abundances of (**A**) zooplankton resting eggs and the total number of resting eggs g^{-1} wet sediment, (**B**) predatory Cladocera resting eggs, (**C**) filtering Cladocera resting eggs, and (**D**) rotifer resting eggs in the 1 cm of sediment layers of Sandöfjärden, Gulf of Finland, Baltic Sea.

Table 1. db-RDA model building for the egg bank data set using sediment nutrient ratios (C : P and C : N), and isotopes of δ^{15}N and δ^{13}C as eutrophication indicators (the sediment model). Jaccard dissimilarity was used and forward selection of environmental variables performed to create the simplest model explaining the variation in the assemblages. The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations).

	DF	AIC	*F*	*p*
+Sediment depth	1	70.92	4.386	0.005**
+δ^{15}N	1	71.16	4.133	0.005**
+Molar C : P	1	72.61	2.605	0.040*
+δ^{13}C	1	73.38	1.822	0.115
+Molar C : N	1	73.39	1.819	0.120

and *Pleopsis* and *Podon* above 17 cm (Fig. 3B). *C. pengoi* resting eggs are present in all but one sample in the uppermost 10 cm sediment layers, the highest relative abundance being at 8–9 cm depth (Fig. 3B). One *C. pengoi* egg is found at 26–27 cm depth. The filtering water fleas *Daphnia* spp. and *B.* (*E.*) *maritima* ephippia are most abundant at the depth of 6–7 cm and fairly abundant in the upper 2 cm (Fig. 3C). In the deeper layers, *B.* (*E.*) *maritima* is more abundant than *Daphnia* spp. and is found evenly throughout the sediment core. Both *Daphnia* spp. and *B.* (*E.*) *maritima* seem to have increased with time. *Ceriodaphnia* spp. ephippia occurs sporadically. As expected, unidentified *Cladocera* spp. follows the abundances of *Ceriodaphnia*, *Daphnia*, and *B.* (*E.*) *maritima*.

Rotifer resting eggs are most abundant at the 4–5 cm depth, and their abundance increases with time (Fig. 3A). *Keratella* spp. resting eggs occur more evenly in all layers than *Synchaeta* spp. resting eggs but lack the clear peak abundance layers (Fig. 3D).

The full db-RDA sediment-model run with the environmental variables δ^{15}N, δ^{13}C, molar C : N, and molar C : P included explains 29.3% of the variation in the egg bank data and is statistically significant ($F_5 = 1.574$, $p = 0.021$). Variance partitioning shows that eutrophication indicators (δ^{13}C, δ^{15}N, C : N, C : P) explain 15.6% of the total variation, sediment depth 5.5% and 8.3% is shared between these two. The effect of autocorrelation between the consecutive samples is thus about one half of the effect of eutrophication. In the best, reduced model, sediment depth is the most significant single explanatory variable, but also δ^{15}N and molar C : P explain a significant part of the variation (Table 1). In the correlation triplot, the only statistically significant axis, the first axis ($F = 4.000$, $p = 0.002$) is associated with eutrophication (Fig. 4A): left oriented vectors are associated with increasing δ^{15}N and C : P ratio and more eutrophic conditions, whereas right oriented vectors are associated with higher δ^{13}C and C : N ratio and less eutrophic conditions, and increasing sediment depth. Of the zooplankton taxa, *Synchaeta* spp. is most strongly correlated with eutrophication, while *Calanoida* spp. and *E. nordmanni* correlate with less eutrophic conditions and deeper sediment layers.

The full db-RDA monitoring-model run with seasonal Chl *a*, salinity, and temperature anomalies included explains 62.5% of the variation in the egg bank data, but is not statistically significant ($F_{10} = 1.023$, $p = 0.456$). Chl *a*, salinity, and temperature anomalies together explain 54.24% of the variation in the egg bank data, year explains 2.47%, and 5.79% of the variation is shared. The effect of autocorrelation between the consecutive samples is thus only about one tenth of the effect of Chl *a*, salinity, and temperature. In the best, reduced db-RDA model, fall Chl *a* is the only statistically significant explanatory variable (Table 2). In the correlation

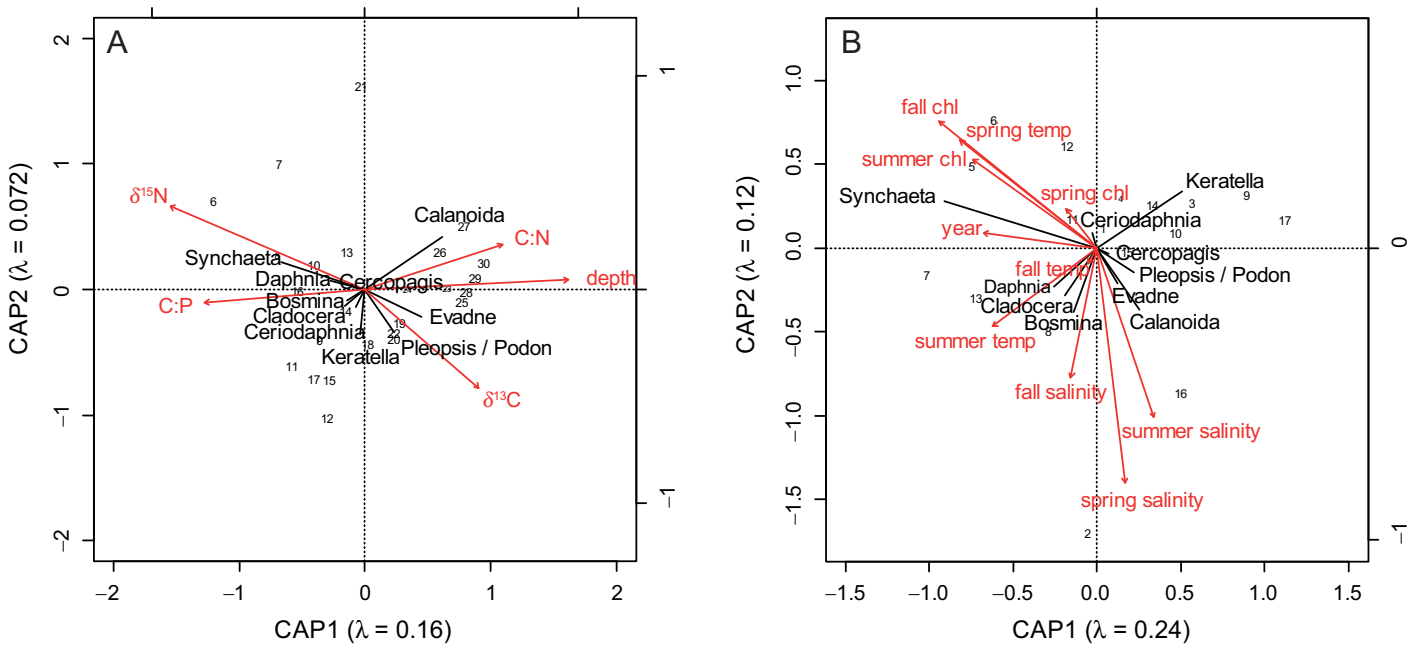

Fig. 4. Correlation triplots based on db-RDA on the relationship between environmental parameters (vectors) and zooplankton community in the sediment layers. Asterisks indicate statistical significance of environmental variables. (**A**) The sediment model explains 29.3% of variation in the data, and the plot with the first two axes display 74% of this variation. (**B**) The monitoring model explains 62.5% of the variation in the data, and the plot displays 57% of this total variation.

Table 2. db-RDA model building for the egg bank data set using seasonal anomalies for Chl *a*, salinity, and temperature as explanatory variables (the monitoring model). Jaccard dissimilarity was used and forward selection of environmental variables performed to create the simplest model explaining the variation in the assemblages. The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations).

	DF	AIC	*F*	*p*
+Fall Chl *a*	1	52.545	2.4818	0.035*
+Spring salinity	1	53.025	1.3091	0.255
+Spring temp	1	53.250	1.4312	0.215
+Fall salinity	1	52.242	2.3220	0.055
+Spring Chl *a*	1	52.434	1.2349	0.265
+Summer Chl *a*	1	52.810	1.0024	0.390
+Summer salinity	1	53.765	0.5757	0.655
+Summer temp	1	54.287	0.7218	0.580
+Fall temp	1	55.562	0.3052	0.875
+Year	1	56.750	0.2936	0.840

triplot, the first axis, which is the only significant axis ($F = 3.853$, $p = 0.014$), is most strongly correlated with time (year) and fall temperature (Fig. 4B). The second axis is nonsignificant and correlates with summer temperature and summer salinity. The rotifer *Synchaeta* spp. is negatively correlated with the first axis and its abundance increases with time, while *Calanoida* spp. is positively correlated and decreases with time.

Bosmina (*Eubosmina*) *maritima* and eutrophication

B. (*E.*) *maritima* ephippia (with or without resting egg) and exoskeletons (headshields, carapaces) revealed similar patterns as *B.* (*E.*) *maritima* resting eggs (Fig. 5): large variations in the abundance of headshields and ephippia between layers, with a long-term trend of increased abundance toward the surface (headshields: 610 $g^{-1} \pm 133$ g^{-1} of sediment [26–30 cm], 2534 $g^{-1} \pm 715$ g^{-1} [6–10 cm]; ephippia: 21 $g^{-1} \pm 4$ g^{-1} [26–30 cm], 151 $g^{-1} \pm 57$ g^{-1} [6–10 cm]). The period of peak abundances is at the depth of 5–8 cm (Fig. 5). The ratio of ephippia to adult carapaces, which indicates the prevalence of sexual to asexual reproduction, does not show any clear long-term trend (10.8 $g^{-1} \pm 1.5$ g^{-1} [26–30 cm], 12.3 $g^{-1} \pm 2.4$ g^{-1} [6–10 cm]). The abundances of *B.* (*E.*) *maritima* headshields, carapaces, and resting eggs (Fig. 5), as well as the overall resting egg abundance of filtering cladocerans (Fig. 3A), are low in those two sediment layers (8–10 cm) which were formed during the time of *C. pengoi* invasion (Fig. 3B). Because of high variation in the abundance of headshields and ephippia between layers, this short-time decrease is not however exceptional.

The full RDA sediment-model run with sediment depth, $\delta^{15}N$, $\delta^{13}C$, molar C : N, molar C : P, and *C. pengoi* resting eggs as explanatory variables explains 64.5% of the variation in the *B.* (*E*) *maritima* data and is statistically significant ($F_6 = 5.46$, $p = 0.001$). The only statistically significant RDA axis, the first axis, is primarily associated with sediment depth and eutrophication ($F = 32.982$, $p = 0.001$). The second

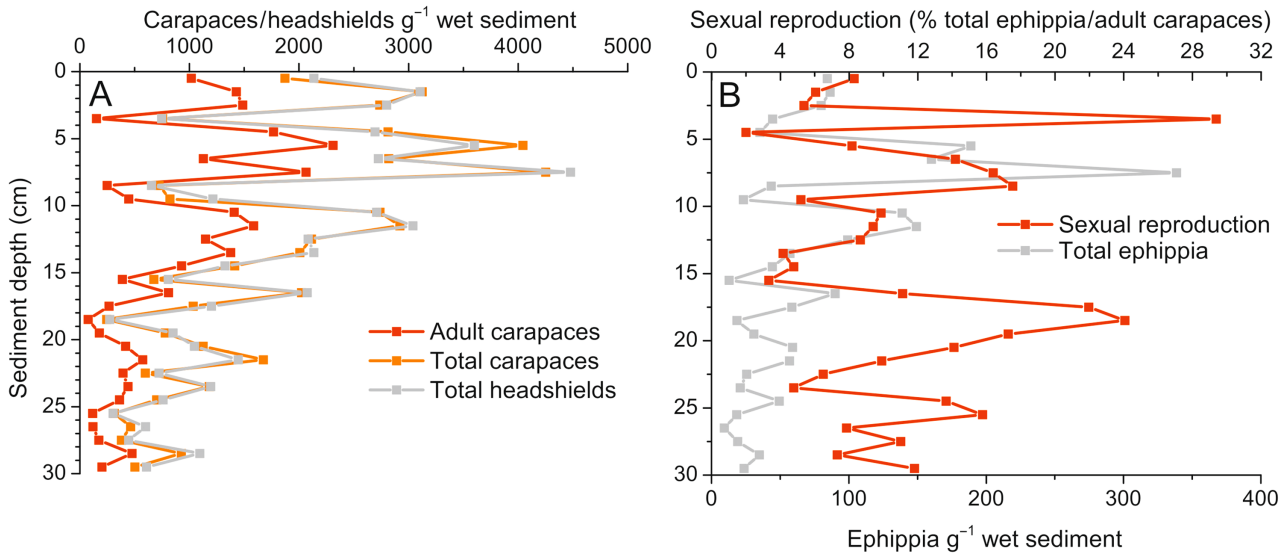

Fig. 5. *Eubosmina maritima* subfossils. Sediment profiles for *E. maritima* cladoceran (**A**) adult carapaces, total carapaces, and total headshields; (**B**) total ephippia (with and without resting egg), and sexual reproduction (total ephippia/adult carapaces).

Table 3. RDA model building for the *Bosmina* data set using sediment nutrient ratios (C : P, C : N), and C and N isotopes as eutrophication indicators (the sediment model). Forward selection of environmental variables was performed to create the simplest model explaining the variation in *Bosmina* abundance and reproduction patterns. The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations).

	DF	AIC	*F*	*p*
+δ^{15}N	1	29.62	16.62	0.005**
+Molar C : P	1	28.65	2.78	0.055*
+*C. pengoi*	1	23.67	6.77	0.005**
+δ^{13}C	1	24.27	1.15	0.335
+Molar C : N	1	25.76	0.39	0.675
+Sediment depth	1	27.31	0.33	0.795

axis is associated with *C. pengoi*. The variables added to the best and reduced models were sediment depth, δ^{13}C and *C. pengoi* (Table 3). The triplot shows a positive association between abundances of *B.* (*E.*) *maritima* headshields, carapaces, and ephippia and the first axis, which reflects eutrophication, whereas sexual reproduction is correlated with the second axis, and thus with *C. pengoi* (Fig. 6A). However, the effect of *C. pengoi* is largely driven by its high abundance at the sediment depth of 9 cm. Variance partitioning of the RDA model reveals high autocorrelation between the consecutive sediment layers: 39.9% of the variation in the *Bosmina* data are explained by the environment (eutrophication and *C. pengoi*) and sediment depth together, and only 24.0% by the environment alone and 0.6% by sediment depth alone.

The full RDA monitoring model run with seasonal Chl *a*, salinity, and temperature anomalies as explanatory variables explains 78.3% of the variation in the *B.* (*E.*) *maritima* data but is statistically nonsignificant ($F_{10} = 2.165$, $p = 0.091$). Variance partitioning of the RDA model reveals that 12.08% of the variation in the *Eubosmina* data is explained by environment and sediment depth together, and 62.6% by environment alone and 3.6% by year. The first axis in the triplot ($F = 30.353$, $p = 0.001$) is mostly associated with primary production (summer and fall Chl *a*, and thus with eutrophication), time (year), and summer water temperature (Fig. 6B). The second axis ($F = 8.666$, $p = 0.002$) is associated with spring and summer salinity, and reversely with summer temperature. Abundance of *Bosmina* ephippia, adult carapaces, total carapaces, and headshields are mostly correlated with the first RDA axis, with eutrophication and high-summer temperature, whereas sexual reproduction correlates more with the second RDA axis, with low-spring and summer salinity and high-summer temperature. The variables added to the best and reduced model were summer temperature and fall chlorophyll (Table 4).

Discussion

Using the archives stored in the sediments, we constructed the eutrophication history of a coastal site in the Baltic Sea during the past six decades, and related changes in environmental conditions to alterations in the zooplankton community as well as to population dynamics of a water flea, *B.* (*E.*) *maritima*. The results reveal an increase in primary productivity since the 1950–1960s, based on nitrogen and carbon concentrations, which is associated with an increased abundance of rotifers, particularly *Synchaeta* spp,

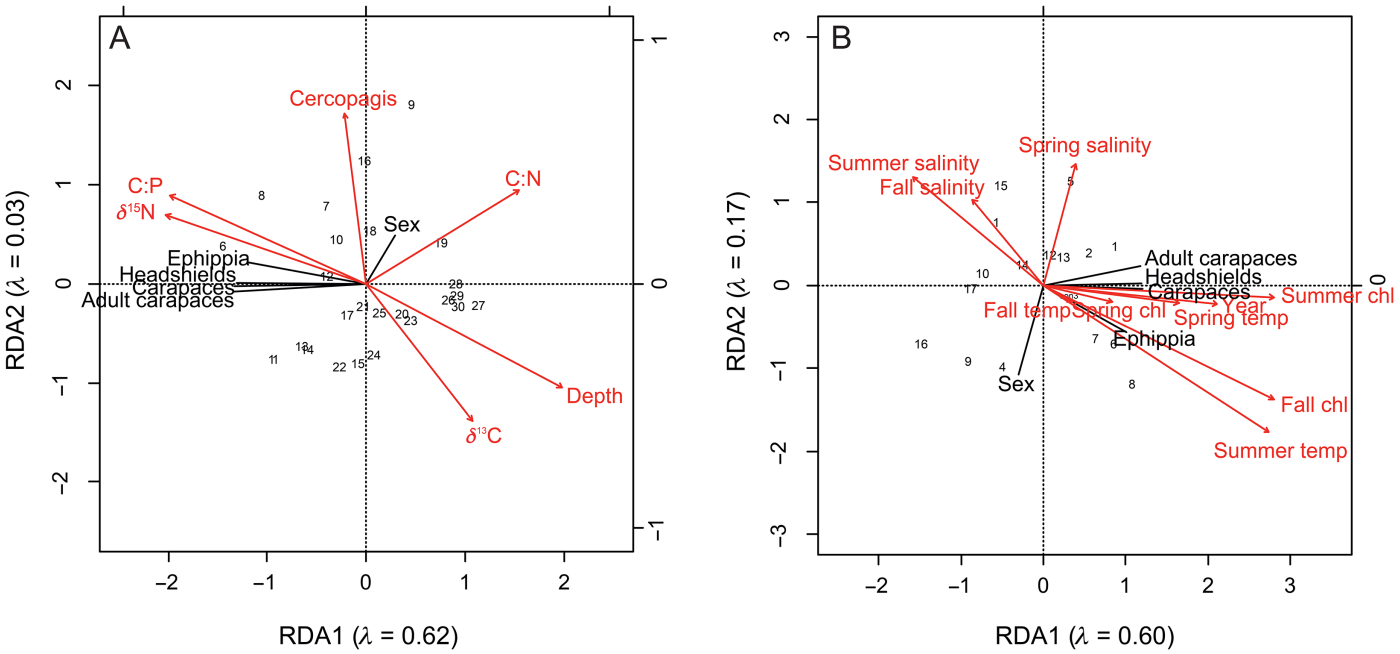

Fig. 6. Correlation plot of the RDAs on the relationship between environmental parameters and *E. maritima* variables in the sediment layers. (**A**) The sediment model (with eutrophication indicators (δ^{13}C, δ^{15}N, C : N, C : P) and *C. pengoi*) explains 64.5% of the variation in the data, and the plot with two axes display 100% of this variation, and (**B**) the monitoring model (with seasonal anomalies of Chl *a*, salinity, and temperature) explains 78.3% of the variation, and the first two axes 98% of this. Interpretation as in Fig. 4.

Table 4. RDA model building for the *Bosmina* data set using seasonal anomalies for Chl *a*, salinity, and temperature as environmental variables (the monitoring model). Forward selection of environmental variables was performed to create the simplest model explaining the variation in *Bosmina* abundance and reproduction patterns. The significance of each environmental variable was tested with a Monte Carlo permutation test (999 unrestricted permutations).

	DF	AIC	*F*	*p*
+Summer temp	1	24.432	6.2209	0.010**
+Fall Chl *a*	1	22.171	3.9881	0.030*
+Spring salinity	1	21.602	2.1210	0.160
+Spring temp	1	20.528	2.3780	0.115
+Summer chl	1	21.045	1.0029	0.385
+Fall temp	1	21.926	0.6804	0.445
+Year	1	21.024	1.6751	0.210
+Summer salinity	1	19.301	1.9587	0.170
+Fall salinity	1	20.798	0.2100	0.865
+Spring chl	1	22.356	0.1581	0.900

and a decreased abundance of calanoid copepods and native predatory water fleas, i.e., a shift toward smaller plankton species.

We excluded the upper 5 cm from our sediment-model analyses, as marine sediments typically have higher concentrations of carbon, nitrogen, and phosphorus in the most recently formed centimeters because of preservation artifacts, regardless of changes in nutrient loading (Cornwell et al. 1996; Vaalgamaa 2004; Vaalgamaa and Korhola 2007). Below the surface sediments, the measurements of TC, TN, and the stable isotopes δ^{15}N and δ^{13}C revealed advancement in productivity since the 1950–1960s. This is in line with results for the Gulf of Finland, which show progressively increased eutrophication since the 1950s (Andersen et al. 2017). The trend is not apparent in our total phosphorous (TP) and organic phosphorus (OP) data, probably due to geochemical remobilization of phosphorous from anoxic sediments (Cornwell et al. 1996). Phosphorous loadings have increased during the time period in the Gulf of Finland (Suikkanen et al. 2013), and the increasing TC : TP ratio with decreasing sediment depth suggests that hypoxia has become more frequent in the area, which accelerates the release of phosphorous during organic-matter breakdown and reduces retention by iron oxides (Jilbert and Slomp 2013). Sedimentary δ^{13}C, which ranged from $-20.6‰$ to $-24.9‰$ suggests that the input of organic matter is, for the most part, of autochthonous origin, since δ^{13}C values for marine sediments range from $-23‰$ to $-18‰$, whereas δ^{13}C values for terrestrial organic matter are lower (Thornton and McManus 1994; Voss et al. 2000). Moreover, the molar C : N ratios of ~ 9 and δ^{15}N values of 3.3–5.3‰ throughout the core are indicatives of autochthonous phytoplankton inputs, such as dinitrogen fixed by cyanobacteria, and limited input of terrestrial organic matter (Voss et al. 2000; Savage et al. 2010).

Thus, the used eutrophication indicators appear to be appropriate proxies of primary production in the area.

According to the db-RDA sediment model performed on the resting egg bank data, the relative shares of calanoid copepods and *Evadne* in the zooplankton community have decreased over time and progressing eutrophication, while the share of rotifers, especially *Synchaeta* spp., has increased along with eutrophication. These results are mostly in line with the results by Suikkanen et al. (2013), showing that plankton communities in the Baltic Sea have shifted toward smaller sized organism between 1979 and 2011 in the Gulf of Finland, with the rotifers *Keratella* spp. and *Synchaeta* spp. as winners, and copepods (*Acartia* spp. and *Eurytemora* spp.) and water fleas (*Bosmina* (*Eubosmina*) spp., *Evadne* spp., and *Podon* spp.) as losers. Our results, however, showed an increase for the relative share of *B*. (*E*.) *maritima* and no notable change in the share of *Keratella* spp. in the zooplankton community. Sampling sites could explain these discrepancies; our sediment cores were sampled from the archipelago, whereas Suikkanen et al. (2013) used monitoring sites on the open sea. In addition, differing hatching condition preferences and senesce between the zooplankton taxa can hamper community reconstruction (De Stasio 2007).

Our sediment model considered only eutrophication as a driver of long-term community changes and explained 29% of the variation in the data. Because much variation could be explained by other abiotic changes, such as in salinity and temperature, we made a model using long-term monitoring data of Chl *a*, seawater temperature and salinity as explanatory variables. This model explained 62.5% of the variation in the zooplankton community, which indicates that all changes are not eutrophication derived. The first two axes of the model were mostly associated with time, temperature and salinity. The model points in the same direction as the sediment model, that the share of *Synchaeta* in the zooplankton community correlates positively, and the shares of calanoid copepods and *Pleopsis/Podon* negatively, with eutrophication, and also with summer and fall primary production. However, the monitoring model is not statistically significant, and, hence, its results should be interpreted with caution. It is based on only 16 observations, since the monitoring data was available only from 1974 onward, and data were lacking for a period in the 1990s. In addition, the surface layer was deleted from the egg bank data.

Eutrophication alters not only zooplankton food quantity, but also quality, which is not reflected in the eutrophication proxies such as Chl *a* and total organic carbon (TOC). Other factors not considered in our two models could have contributed to the changes in the zooplankton community. In particular, the zooplankton predation regime has changed during the studied period. Changes in the North Atlantic Oscillation (NAO) index increased air and sea surface temperatures in the late 1980s, which affected trophic levels from phytoplankton to fish (Alheit et al. 2005). Simultaneously Baltic cod, the main top predator of the pelagic food web, decreased due to reduced salinity and increased fishing pressure, and the effect cascaded down the food web to zooplankton and phytoplankton (Casini et al. 2008). The only notable contemporary change (above depth 17 cm) is the increased abundance of *Pleopsis*/*Podon* spp. eggs in relation to *E. nordmanni*. Both *Podon* spp. and *E. nordmanni* benefit from warmer seawater (Dippner et al. 2000; Möllmann et al. 2002). We were not able to differentiate between *Pleopsis* spp. and *Podon* spp., thus the shift could be driven by changes in only one of the species.

The abundance of *B*. (*E*.) *maritima* has increased in the study area during the investigated time period, based on the number of ephippia and exoskeleton remains in the sediment layers, which suggests favorable growth conditions. Life-history traits of water fleas are known to be flexible and vary in response to changes in the quantity and quality of resources (Urabe and Sterner 2001; Acharya et al. 2005) as well as in predation pressure (Kerfoot 1987; Jankowski 2004). During favorable conditions, fecundity is high, and *Bosmina* populations can grow rapidly through parthenogenesis (Kankaala and Wulff 1981; Hanazato and Yasuno 1987). A similar increase in abundance with eutrophication has been detected in *B*. (*E*.) *maritima* population in the Central Baltic Sea (Struck et al. 1998). As an efficient filter feeder, *B*. (*E*.) *maritima* benefits from high primary production (Kankaala and Wulff 1981; Urabe 1991), and may tolerate, and even exploit, toxic cyanobacteria blooms (Sun et al. 2012; Jiang et al. 2014).

The invasive predatory water flea *C. pengoi* had a negative effect on the annual mean abundance of *B*. (*E*.) *maritima* populations during its invasion (Ojaveer et al. 2004). Our data show a possible small, short-time decrease in the abundance of *B*. (*E*.) *maritima* and other filtering cladocerans at the time of invasion, which does not, however, appear in the statistical models. In the sediment model RDA, the prevalence of sexual to asexual reproduction of *B*. (*E*.) *maritima* was associated with introduction of *C. pengoi*, which can be detected based on the appearance of *C. pengoi* resting eggs to the sediment layers (Katajisto et al. 2013). This suggests that *B*. (*E*.) *maritima* intensified its sexual reproduction in response to the invasion. Sexually produced resting eggs are an overwintering strategy for the Baltic Sea cladocerans (Viitasalo et al. 1995; Katajisto et al. 1998), and their production can be triggered by factors such as high-population densities (Kankaala 1983; Põllupüü et al. 2010). Other stimuli that can induce sexual reproduction on cladocerans include eutrophication, pollution, and changes in predation pressure (Kleiven et al. 1992; Ślusarczyk 1995, 1999; Nevalainen et al. 2011*a*; Lampert et al. 2014). For instance, subfossil records of chydorids (Cladocera) from lakes in Finland suggest that ephippia production is promoted by eutrophication, acidification, and aluminum pollution (Nevalainen et al. 2011*b*). In

Norwegian lakes, the illegal introduction of perch to a lake previously lacking planktivorous pelagic fishes increased genotypic diversity of the cladoceran *Daphnia pulex*, most likely through enhanced sexual reproduction (Lampert et al. 2014). Our result of increased ephippia production in *Bosmina* coinciding with *C. pengoi* invasion is largely based on one sediment layer (9 cm) with the highest number of *C. pengoi* resting eggs.

The RDA monitoring model gave the same indication as the sediment model that *B.* (*E.*) *maritima* benefits from high-primary production and, thus, from eutrophication; its abundance (carapaces, ephippias, headshields) was positively correlated with summer and fall Chl *a*. Sexual reproduction was mostly positively correlated with summer temperature and negatively correlated with spring and summer salinity. Favorable spring and summer conditions—high temperature, and low salinity—could have promoted the growth of the population, while crowding and/or the invasion of the predatory water flea could have triggered sexual reproduction. However, the results should be interpreted with caution since the monitoring model is not statistically significant.

The reconstruction of the past zooplankton community was based on the sampling of a site with periodic anoxia, as this reduces the loss of dormant eggs through hatching, predation, and bioturbation by benthic animals. However, other factors could have influenced community reconstruction, such as differences in preferred hatching conditions among species and senescence. The much higher copepod egg abundance in the surface sediment than in deeper layers implies that a large proportion of the copepod eggs hatch before the site turns hypoxic in the spring, but that hatching had not yet taken place at the time of sampling. For the water fleas and rotifers, the number of resting eggs found in the surface sediment did not differ dramatically from the layers below. However, only 1% or less of the *E. maritima* ephippia contained an egg. If the eggs had decomposed in the sediment or been empty or malformed since their production needs further investigation.

To summarize, our results indicate that gradual eutrophication during the recent decades at a coastal site in the Baltic Sea has altered the zooplankton community. There has been a shift toward smaller plankton species like rotifers, whereas abundances of calanoid copepods and predatory water fleas have decreased. *B.* (*E.*) *maritima* seems to have benefitted from eutrophication, which is reflected in increased number of subfossils and resting eggs in the more recent sediment layers compared to the older ones. Sediment record suggest that *B.* (*E.*) *maritima* responded to the invasion of the predatory water flea *C. pengoi* with a short-term increase in sexual reproduction. The invasion and the following increased predation pressure had possibly also a short-term negative effect on the abundance of *B.* (*E.*) *maritima* and other filtering cladocerans. Otherwise, the invasion did not seem to have notable effects on the zooplankton community. Moreover, the results show that resting egg banks at periodically anoxic sites can give similar information about community changes as zooplankton monitoring at regional scales.

References

Acharya, K., J. D. Jack, and P. A. Bukaveckas. 2005. Dietary effects on life history traits of riverine Bosmina. Freshwat. Biol. **50**: 965–975. doi:10.1111/j.1365-2427.2005.01379.x

Alheit, J., C. Möllmann, J. Dutz, G. Kornilovs, P. Loewe, V. Morholz, and N. Wasmund. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES J. Mar. Sci. **62**: 1205–1215. doi:10.1016/j.icesjms.2005.04.024

Andersen, J. H., and others. 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. Biol. Rev. **92**: 135–149. doi:10.1111/brv.12221

Barnosky, A. D., and others. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science **355**: eaah4787. doi:10.1126/science.aah4787

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. **15**: 365–377. doi:10.1111/j.1461-0248.2011.01736.x

Birks, H. J. B. 2012. Analysis of stratigraphical data, p. 355–378. *In* H. J. B. Birks, A. F. Lotter, S. Juggins, and J. P. Smol [eds.], Tracking environmental change using lake sediments. Springer.

Błędzki, L. A., and J. I. Rybak. 2016. Freshwater crustacean zooplankton of Europe: Cladocera & copepoda (calanoida, cyclopoida) key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer.

Brendonck, L., and L. De Meester. 2003. Egg banks in freshwater zooplankton: Evolutionary and ecological archives in the sediment. Hydrobiologia **491**: 65–84. doi:10.1023/A:1024454905119

Carman, R., and H. Cederwall. 2001. Sediments and macrofauna in the Baltic Sea—Characteristics, nutrient contents and distribution, p. 289–327. *In* F. Wulff, L. Rahm, and P. Larsson [eds.], A system analysis of the Baltic Sea. Springer.

Casini, M., J. Lövgren, M. Hjelm, M. Cardinale, J. Molinero, and G. Kornilovs. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proc. R. Soc. Lond. B. Biol. Sci. **275**: 1793–1801. doi:10.1098/rspb.2007.1752

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. **210**: 223–253. doi:10.3354/meps210223

Cornwell, J., D. Conley, M. Owens, and J. Stevenson. 1996. A sediment chronology of the eutrophication of Chesapeake Bay. Estuaries **19**: 488–499. doi:10.2307/1352465

Decaestecker, E., L. De Meester, and J. Mergeay. 2009. Cyclical parthenogenesis in *Daphnia*: Sexual versus asexual reproduction, p. 295–316. *In* I. Schön, K. Martens, and P. van Dijk [eds.], Lost sex. Springer.

De Stasio, B. T. 1989. The seed bank of a fresh-water crustacean—Copepodology for the plant ecologist. Ecology **70**: 1377–1389. doi:10.2307/1938197

De Stasio, B. T. 2007. Egg bank formation by aquatic invertebrates: A bridge across disciplinary boundaries, p. 121–133. *In* V. R. Alekseev, B. T. De Stasio, and J. J. Gilbert [eds.], Diapause in aquatic invertebrates—Theory and human use. Springer.

Dietl, G. P., S. M. Kidwell, M. Brenner, D. A. Burney, K. W. Flessa, S. T. Jackson, and P. L. Koch. 2015. Conservation paleobiology: Leveraging knowledge of the past to inform conservation and restoration. Ann. Rev. Earth Planet. Sci. **43**: 79–103. doi:10.1146/annurev-earth-040610-133349

Dippner, J. W., G. Kornilovs, and L. Sidrevics. 2000. Long-term variability of mesozooplankton in the Central Baltic Sea. J. Mar. Syst. **25**: 23–31. doi:10.1016/S0924-7963(00)00006-3

Dirzo, R., H. S. Young, M. Galetti, G. Ceballo, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science **345**: 401–406. doi:10.1126/science.1251817

Elmgren, R. 2001. Understanding human impact on the Baltic ecosystem: Changing views in recent decades. AMBIO **30**: 222–231. doi:10.1579/0044-7447-30.4.222

Hairston, N. G. Jr. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. Limnol. Oceanogr. **41**: 1087–1092. doi:10.4319/lo.1996.41.5.1087

Hairston, N. G., R. A. Van Brunt Jr., C. M. Kearns, and D. R. Engstrom. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. Ecology **76**: 1706–1711. doi:10.2307/1940704

Harley, C. D., and others. 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. **9**: 228–241. doi:10.1111/j.1461-0248.2005.00871.x

Hanazato, T., and M. Yasuno. 1987. Experimental studies on competition between *Bosmina longirostris* and *Bosmina fatalis*. Hydrobiologia **154**: 189–199. doi:10.1007/BF00026839

Jackson, S. T., and J. L. Blois. 2015. Community ecology in a changing environment: Perspectives from the Quaternary. PNAS **112**: 4915–4921. doi:10.1073/pnas.1403664111

Jankowski, T. 2004. Predation of freshwater jellyfish on *Bosmina*: The consequences for population dynamics, body size, and morphology. Hydrobiologia **530–531**: 521–528. doi:10.1007/s10750-004-2648-6

Jiang, X., W. Yang, L. Zhang, L. Chen, and Y. Niu. 2014. Predation and cyanobacteria jointly facilitate competitive dominance of small-bodied cladocerans. J. Plankton Res. **36**: 956–965. doi:10.1093/plankt/fbu032

Jilbert, T., and C. P. Slomp. 2013. Rapid high-amplitude variability in Baltic Sea hypoxia during the Holocene. Geology **41**: 1183–1186. doi:10.1130/G34804.1

Kankaala, P. 1983. Resting eggs, seasonal dynamics, and production of *Bosmina longispina maritima* (Muller,p.E.) (Cladocera) in the Northern Baltic Proper. J. Plankton Res. **5**: 53–69. doi:10.1093/plankt/5.1.53

Kankaala, P., and F. Wulff. 1981. Experimental studies on temperature-dependent embryonic and post-embryonic developmental rates of *Bosmina longispina maritima* (Cladocera) in the Baltic. Oikos **36**: 137–146. doi:10.2307/3544438

Katajisto, T., M. Viitasalo, and M. Koski. 1998. Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. Mar. Ecol. Prog. Ser. **163**: 133–143. doi:10.3354/meps163133

Katajisto, T., L. Karjala, and M. Lehtiniemi. 2013. Fifteen years after invasion: Egg bank of the predatory cladoceran *Cercopagis pengoi* in the Baltic Sea. Mar. Ecol. Prog. Ser. **482**: 81–92. doi:10.3354/meps10266

Kennish, M. 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. **29**: 78–107. doi:10.1017/S0376892902000061

Kerfoot, W. C. 1987. Translocation experiments—*Bosmina* responses to copepod predation. Ecology **68**: 596–610. doi:10.2307/1938465

Kleiven, O. T., P. Larsson, A. Hobæk, and A. Hobaek. 1992. Sexual reproduction in *Daphnia magna* requires 3 stimuli. Oikos **65**: 197–206. doi:10.2307/3545010

Kidwell, S. M. 2015. Biology in the Anthropocene: Challenges and insights from young fossil records. PNAS **112**: 4922–4929. doi:10.1073/pnas.1403660112

Korhola, A., and M. Rautio. 2001. Cladocera and other branchiopod crustaceans, p. 5–41. *In* J. P. Smol, H. J. B. Birks, and W. M. Last [eds.], Tracking environmental change using lake sediments, zoological indicators. Kluwer.

Koroleff, F. 1976. Determination of nutrients: 1. Phosphorus, p. 117–126. *In* K. Grasshoff [eds.], Methods of seawater analysis. Verlag Chemie.

Korosi, J. B., J. Kurek, and J. P. Smol. 2013. A review on utilizing *Bosmina* size structure archived in lake sediments to infer historic shifts in predation regimes. J. Plankton Res. **35**: 444–460. doi:10.1093/plankt/fbt007

Kotov, A. A., Ishida, S. S. Taylor. D. J. 2009. Revision of the genus Bosmina Baird, 1845 (Cladocera: Bosminidae), based on evidence from male morphological characters and molecular phylogenies. Zool. J. Linn. Soc. **156**: 1–51. doi:10.1111/j.1096-3642.2008.00475.x

Lampert, K. P., B. P. Regmi, I. Wathne, and P. Larsson. 2014. Clonal diversity and turnover in an overwintering *Daphnia pulex* population, and the effect of fish predation. Freshwat. Biol. **59**: 1735–1743. doi:10.1111/fwb.12378

Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. **69**: 1–24. doi:10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Legendre, P. and L. Legendre. 1998. Numerical ecology. 2nd English ed. Elsevier.

Levin, L. A., and others. 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences **6**: 2063–2098. doi:10.5194/bg-6-2063-2009

Maguire, K. C., D. Nieto-Lugilde, M. C. Fitzpatrick, J. W. Williams, and J. L. Blois. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. Ann. Rev. Ecol. Evol. Syst. **46**: 343–368. doi:10.1146/annurev-ecolsys-112414-054441

Möllmann, C., F. Köster, G. Kornilovs, and L. Sidrevics. 2002. Long-term trends in abundance of cladocerans in the Central Baltic Sea. Mar. Biol. **141**: 343–352. doi:10.1007/s00227-002-0822-9

Moritz, C., and R. Agudo. 2013. The future of species under climate change: Resilience or decline? Science **341**: 504–508. doi:10.1126/science.1237190

Nevalainen, L., K. Sarmaja-Korjonen, M. Gasiorowski, and T. P. Luoto. 2011*a*. Late 20(th) century shifts in cladoceran community structure and reproduction in an acidified boreal lake. Fund. Appl. Limnol. **179**: 81–92. doi:10.1127/1863-9135/2011/0179-0081

Nevalainen, L., T. P. Luoto, S. Levine, and M. Manca. 2011*b*. Paleolimnological evidence for increased sexual reproduction in chydorids (Chydoridae, Cladocera) under environmental stress. J. Limnol. **70**: 255–262. doi:10.4081/jlimnol.2011.255

Ojaveer, H., M. Simm, A. Lankov, and A. Lumberg. 2000. Consequences of invasion of a predatory cladoceran. ICES J. Mar. Sci. CM 2000/U: 16.

Ojaveer, H., M. Simm, and A. Lankov. 2004. Population dynamics and ecological impact of the non-indigenous *Cercopagis pengoi* in the Gulf of Riga (Baltic Sea). Hydrobiologia **522**: 261–269. doi:10.1023/B:HYDR.0000029927.91756.41

Ojaveer, H., and others. 2010. Status of biodiversity in the Baltic Sea. PLoS One **5**: e12467. doi:10.1371/journal.pone.0012467

Ojaveer, H., and J. Kotta. 2015. Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: Literature survey evidences major limitations in knowledge. Hydrobiologia **750**: 171–185. doi:10.1007/s10750-014-2080-5

Oksanen, J. F. G., and others. 2016. Vegan: Community ecology package. R package version 2.4-1. Available from https://CRAN.R-project.org/package=vegan

Põllupüü, M., M. Simm, and H. Ojaveer. 2010. Life history and population dynamics of the marine cladoceran *Pleopis polyphemoides* (Leuckart) (Cladocera, Crustacea) in a shallow temperate Pärnu Bay (Baltic Sea). J. Plankton Res. **32**: 1459–1469. doi:10.1093/plankt/fbq063

Purasjoki, K. J. 1958. Zur Biologie der Brackwasserkladozere *Bosmina coregoni maritima* (P. E. Müller). Ann. Zool. Soc. **19**: 1–117. http://hdl.handle.net/10138/168817

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org

Savage, C., P. R. Leavitt, and R. Elmgren. 2010. Effects of land use, urbanization, and climate variability on coastal eutrophication in the Baltic Sea. Limnol. Oceanogr. **55**: 1033–1046. doi:10.4319/lo.2010.55.3.1033

Scheffers, B. S., and others. 2016. The broad footprint of climate change from genes to biomes to people. Science **354**: aaf7671. doi:10.1126/science.aaf7671

Ślusarczyk, M. 1995. Predator-induced diapause in *Daphnia*. Ecology **76**: 1008–1013. doi:10.2307/1939364

Ślusarczyk, M. 1999. Predator-induced diapause in *Daphnia magna* may require two chemical cues. Oecologia **119**: 159–165. doi:10.1007/s004420050772

Solórzano, L., and J. H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural water? Limnol. Oceanogr. **25**: 754–758. doi:10.4319/lo.1980.25.4.0754

Struck, U., M. Voss, B. von Bodungen, and N. Mumm. 1998. Stable isotopes of nitrogen in fossil cladoceran exoskeletons: Implications for nitrogen sources in the central Baltic Sea during the past century. Naturwissenschaften **85**: 597–603. doi:10.1007/s001140050558

Sun, X. X., M. Tao, B. Q. Qin, M. Qi, Y. Niu, J. Zhang, Z. M. Ma, and P. Xie. 2012. Large-scale field evidence on the enhancement of small-sized cladocerans by *Microcystis* blooms in Lake Taihu, China. J. Plankton Res. **34**: 853–863. doi:10.1093/plankt/fbs047

Suikkanen, S., S. Pulina, J. Engström-Öst, M. Lehtiniemi, S. Lehtinen, and A. Brutemark. 2013. Climate change and eutrophication induced shifts in northern summer plankton communities. PLoS One **8**: e66475. doi:10.1371/journal.pone.0066475

Thornton, S., and J. McManus. J. 1994. Application of organic-carbon and nitrogen stable-isotope and C/N ratios as source indicators of organic-matter provenance in estuarine systems—Evidence from the Tay Estuary, Scotland. Estuar. Coast. Shelf Sci. **38**: 219–233. doi:10.1006/ecss.1994.1015

Urabe, J. 1991. Effect of food concentration on growth, reproduction and survivorship of *Bosmina longirostris* (Cladocera)—An experimental study. Freshwat. Biol. **25**: 1–8. doi:10.1111/j.1365-2427.1991.tb00467.x

Urabe, J., and R. W. Sterner. 2001. Contrasting effects of different types of resource depletion on life-history traits in *Daphnia*. Funct. Ecol. **15**: 165–174. doi:10.1046/j.1365-2435.2001.00511.x

Vaalgamaa, S. 2004. The effect of urbanisation on Laajalahti Bay, Helsinki City, as reflected by sediment geochemistry. Mar. Pollut. Bull. **48**: 650–662. doi:10.1016/j.marpolbul.2003.10.008

Vaalgamaa, S., and A. Korhola. 2007. Geochemical signatures of two different coastal depositional environments within the same catchment. J. Paleolimnol. **38**: 241–260. doi:10.1007/s10933-006-9071-0

Vallius, H. 2006. Permanent seafloor anoxia in coastal basins of the northwestern Gulf of Finland, Baltic Sea. AMBIO **35**: 105–108. doi:10.1579/0044-7447(2006)35[105:PSAICB]2.0.CO;2

Viitasalo, M., and T. Katajisto. 1994. Mesozooplankton resting eggs in the Baltic Sea: Identification and vertical distribution in laminated and mixed sediments. Mar. Biol. **120**: 455–465. doi:10.1007/BF00680221

Viitasalo, M., I. Vuorinen, and S. Saesmaa. 1995. Mesozooplankton dynamics in the Northern Baltic Sea—Implications of variations in hydrography and climate. J. Plankton Res. **17**: 1857–1878. doi:10.1093/plankt/17.10.1857

Voss, M., B. Larsen, M. Leivuori, and H. Vallius. 2000. Stable isotope signals of eutrophication in Baltic Sea sediments. J. Mar. Syst. **25**: 287–298. doi:10.1016/S0924-7963(00)00022-1

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **365**: 2019–2024. doi:10.1098/rstb.2010.0021

Warner, R., and P. Chesson. 1985. Coexistence mediated by recruitment fluctuations—A field guide to the storage effect. Am. Nat. **125**: 769–787. doi:10.1086/284379

Zuur, A. F., E. N. Ieno, and C. S. Elphic. 2009. A protocol for data exploration to avoid common statistical problems. Meth. Ecol. Evol. **1**: 3–14. doi:10.1111/j.2041-210X.2009.00001.x

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Conflict of Interest

None declared.

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